1936

Genetical and histological studies of fruit size and shape in the tomato

Albert Franklin Yeager
Iowa State College

GENETICAL AND HISTOLOGICAL STUDIES OF FRUIT SIZE AND SHAPE IN THE TOMATO

By

ALBERT FRANKLIN YEAGER

A Thesis Submitted to the Graduate Faculty
for the Degree of

DOCTOR OF PHILOSOPHY

Major Subject Genetics

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State College
1936

UMI Number: DP13070

UMI®

UMI Microform DP13070

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

TABLE OF CONTENTS

	Page
INTRODUCTION	3
HISTORICAL	4
MATERIALS AND METHODS	6
EXPERIMENTAL	8
The Development of Shape	22
Another Oval Fruit Shape	26
DISCUSSION	33
CONCLUSIONS	37
LITERATURE CITED	38
ACKNOWLEDGMENT	40
VITA	41

INTRODUCTION

This investigation is concerned with the inheritance and the development of fruit size and shape in tomatoes (Lycopersicum). Locule number of the fruit, because of its apparent association with size and shape was given special attention.

HISTORICAL

The tomato was one of the early plants used in genetical studies after the rediscovery of Mendel's law, and shape was among the first characters mentioned. Hedrick and Booth (4) as early as 1907 list a shape factor. Price and Drinkard (14) mention round as dominant to pear shape, round-conic dominant to round-compressed, two-celled fruit dominant to many celled, and smooth surface dominant to rough. Various hypotheses have been advanced as to the number and relation of genes to size and shape. Frimmel (2) says that fruit size is complex, depending on carpel size and the degree of fasciation, with carpel size intermediate in F_1, fasciation recessive. Leslie and Rosa (7) state that oblateness is inevitable for size. Lindstrom (8) reports genes Pp and Yy linked with a major size factor. Later (9, 10) he suggests as allelomorphs oval, round and oblate linked with Dd and Pp, and reports shape and size correlated. MacArthur (13) gives ten linkage groups involving 20 genes, but does not include locule number as one of these. Currence (1) reports significant association between fasciation and fruit size, suggesting that factors affecting fruit contour probably also affect size.

Sinnott (16), working with Cucurbita, traced the histological development of shape and size. He found shape determined in the earliest primordia of the pistillate flower, and that cell division in the ovary had ceased by anthesis. Houghtaling's (5) studies with tomato have supplied the reason for the correlations between ovary and fruit measurements reported by Hackbarth et al. (3) in crosses between L. esculentum and L. racemigerum. She found that a differential rate of growth occurs at earliest primordia, ceasing in L. esculentum at anthesis, at which time cell division is complete.

There has been some confusion in the use of terms. The fasciation reported by Frimmel (2), Warren (18) and Houghtaling (5) evidently refers to an increase in the number of locules or, as Price and Drinkard (14) call them, cells. On the other hand, Currence (1) and MacArthur (12) in calculating linkages between fasciated fruits and leafy inflorescence refer to rough fruit without regard to locule number. Such confusion is easily accounted for by the fact that in the many loculed fruits roughness is much more easily seen.

MATERIALS AND METHODS

The seed stocks used in this work were procured from the following sources: The Department of Genetics, Iowa State College; the Department of Horticulture, North Dakota Agricultural College; and commercial seedsmen. Fruit shape, i.e. polar and equatorial diameter ratio, was determined, unless otherwise stated, by the use of calipers. Locule number was determined by sectioning. Ovary measurements were made by the use of a low power microscope and an eye piece micrometer. Wherever possible, the mean of ten fruits was used in determining fruit and ovary shape, and locule number.

In this investigation we shall deal with locule number, using the suggested gene symbols Lc (few) and lc (many) locules as distinct from the Ff (rough fruit or fasciation) genes. For reasons given later tomatoes with an average of 3.5 or more locules are classed as lc.

For shape, o (oval) will be used to indicate a polar diameter 1.2 or more times the equatorial diameter, O (round) for a ratio of .95-1.2, and O' (oblate) for a ratio less than .95. O' is used for convenience only, since such plants do not necessarily differ genetically from O, inasmuch as the existence of this suggested allelomorph has not yet been proven.

Standard error rather than probable error is used. In all correlations, * indicates a significant correlation and ** a highly significant one, as calculated from Table 16 in "Correlation and Machine Calculation" by Wallace and Snedecor (17).

The following known genes are involved in this study:

Dd	Standard-dwarf plants
Oo	Oblate-oval fruits
Ss	Simple-compound flower cluster
Rr	Red-yellow fruit
Yy	Yellow-clear skin
Spsp	Indeterminate-self pruning plants
Cc	Cut-potato leaf
Aa	Purple-green stem
Ll	Green-lutescent foliage

EXPERIMENTAL

Quantitative characters may often best be studied by determining whether they are associated with qualitative ones. It was decided to approach locule number in this way. Crosses were therefore made in which the parental stocks differed in locule number and in other characters which could be separated readily. F_2 and back cross progenies were then classified according to these qualitative characters, and their relation to mean locule number determined.

In Table I-A, B and C will be seen such tabulated F_2 generations and back crosses. In these it may be noted that there is a significant association between locule number and the first chromosome linked genes Dd Oo Ss, but no association with the Rr gene. In B, the back cross population is divided into two classes O (round) and O' (oblate), rather than o and O, because the plant used in test crossing was oblate, producing when crossed with o, a round fruit, and when crossed with O, an oblate fruit.

Populations D, E, F and G show dwarf coming into the cross associated with many locules which is the reverse of the crosses in A, B and C, but again there is a significant association between locule number and Dd, but no significant association with Rr and Cc. Population H involves Yy, and here again there is no evidence of association. This close association between genes of the first chromosome and locule number does not, however, prove the existence of any gene for locule number. Locule number might perhaps be an indirect effect of the shape gene, or of size previously reported as associated with first chromosome genes by Lindstrom (10).

As a means of studying the relation of locule number to shape and fruit weight, correlations were calculated between these characters in several F_2 and back cross populations. These are shown in Table II. In A and B the larger parental varieties also have the greater number of locules. The progenies in every case exhibit highly significant correlations between size and locule number; shape, i.e. $\frac{\text{equatorial diameter}}{\text{polar diameter}}$, and locule number; and shape and weight. This is true even in A where the large, many-loculed parental variety has oval fruits. No explanation is offered at this point for this situation. It is presented merely to emphasize the point that there is a strong tendency for many loculed fruits to be oblate.

Data from crosses between comparatively large tomatoes with few locules and smaller, many-loculed ones would seem to afford some possible clue as to the causal relationship between size, shape and locule number. Small, many loculed varieties not being available an attempt was made to produce them. Crosses were therefore made between Bison, a large, many-loculed

TABLE I

Association of certain tomato characteristics with locule number

Parents	Phenotypic Segregates		Mean Number of Locules	Difference	P
A - F_2	197	D	3.21	.70±.09	.01-
	55	d	2.51		
(26) D O S lc / (3) d o s Lc	211	S	3.16	.52±.10	.01-
	41	s	2.64		
	134	O	3.33	.94+.08	.01-
	46	o	2.42		
B - Backcross	28	D	4.61	.58±.11	.01-
	23	d	4.03		
(26) D O R lc / (3) d o r Lc x (46) d O' r lc / d O' r lc	32	O	4.12	.44±.06	.01-
	19	O'	4.56		
	18	R	4.36	.02±.13	.88
	33	r	4.34		
C - F_2 (Bison) O lc / (Yellow Pear) o Lc	138	O	3.24	.69±.10	.01-
	44	o	2.55		
D - Backcross (49) d lc / (9) D Lc x (40) d lc / d lc	45	D	3.90	.57±.14	.01-
	64	d	4.47		
E - Backcross	95	D	4.23	.49±.19	.01
	80	d	4.72		
(40) d O' r lc x (49) d O' r lc	81	R	4.46	[illegible]	[illegible]

	18 33	R r	4.36 4.34	.02±.13	.88
C - F_2 $\dfrac{\text{(Bison)} \quad \text{O lc}}{\text{(Yellow Pear)} \quad \text{o Lc}}$	138 44	O o	3.24 2.55	.69±.10	.01-
D - Backcross $\dfrac{(49) \quad \text{d lc}}{(9) \quad \text{D Lc}} \times (40) \dfrac{\text{d lc}}{\text{d lc}}$	45 64	D d	3.90 4.47	.57±.14	.01-
E - Backcross	95 80	D d	4.23 4.72	.49±.19	.01
$(40) \dfrac{\text{d O' r lc}}{\text{d O' r lc}} \times \dfrac{(49) \quad \text{d O' r lc}}{(9) \quad \text{D o R Lc}}$	81 94	R r	4.46 4.47	.01±.16	.90
	96 79	O O	4.26 4.80	.54±.13	.01-
F - Backcross	32 33	D d	3.48 4.09	.61±.15	.01-
$\dfrac{(49) \quad \text{c d lc}}{(10) \quad \text{C D Lc}} \times (49) \dfrac{\text{c d lc}}{\text{c d lc}}$	34 31	C c	3.85 3.77	.08±.15	.69
G - Backcross $\dfrac{(9) \quad \text{D Lc}}{(34) \quad \text{d lc}} \times (49) \dfrac{\text{d lc}}{\text{d lc}}$	59 41	D d	2.45 3.23	.78±.11	.01-
H - F_2 $\dfrac{(47) \quad \text{Y Lc}}{(48) \quad \text{y lc}}$	103 32	Y y	5.59 5.68	.09±.13	.53

oblate tomato, and Red Currant, a few-loculed, round one; and also between Bison and Yellow Cherry. These, carried through several generations, did give pure oblate strains with many locules which had smaller fruits (42 grams) than those of the largest two-loculed oval varieties (56 grams). The fact that the synthesis of such varieties was possible is an indication that locule number is not a mere secondary effect of size. These synthesized varieties did not, however, have smaller locules than those of the small two-loculed parent but appeared to consist of a larger number of the small locules and therefore did not approach the Red Currant variety in weight. Likewise, the large, two-loculed variety, while very large for a two-loculed sort, did not approach the weight of the common, many-loculed, large ones except in weight per locule. C in Table II shows an F_2 of the cross between such a small, many-loculed tomato and a few-loculed, large one. In determining shape correlations the ratio of $\frac{\text{equatorial diameter}}{\text{polar diameter}}$ was used as a shape index, with classes from .60 to 1.80 at .10 intervals. D and E show the F_1 of such a cross back-crossed to large, many-loculed forms. It may be noted that while correlations exist, they are very small in the case of weight and shape, except in E where the population is small and the correlations not highly significant. The correlations between locules and weight are likewise not significant in C, D and E where the smaller parent is many-loculed. This is in contrast

TABLE II

Correlations between locules, weight and shape in various F_2 and back cross populations.

	Number of Plants	Pedigree	Weight and Locule Number	Weight and Shape	Locule Number and Shape
A	207	(Ohio Red) Large, oval lc / (Yellow Cherry) Small, round Lc F_2	.76**	.30**	.42**
B	76	(Oxheart) Large lc / (Yellow Cherry) Small Lc F_2	.51**	.37**	.47**
C	28	(9) Large o Lc / (36) Small O lc F_2	.32	.06	.85**
D	47	(9) Large o Lc / (36) Small O lc x (40) Large O lc / Large O lc	.17	.00	.31*
E	15	(10) Large o Lc / (36) Small O lc x (40) Large O lc / Large O lc	.15	.58*	.46

to the situation in A and B when the large-fruited parent is many-loculed and such correlations highly significant.

Partial correlations may be useful in studying the relation between size, shape and locule number. Such correlations as those presented in Table III show that where the parental lc stock is the smaller fruited the correlation between shape and locule number is practically unchanged by eliminating weight; that the correlation between locules and weight likewise remains about the same, but that the correlation between weight and shape becomes distinctly negative when locule effect is removed, thus indicating that weight and shape are associated because of their mutual association with locule number. These data throw much doubt on the possibility of oblate shape being in itself the cause of large size. A possible hypothesis would be that the small locules in the oblate parent tend to remain associated with oblateness in the progenies and to cause the oblate tomatoes in the F_2 and test crosses to be smaller, while the many locules carried by the same parent tend to increase the size of tomatoes possessing this character.

Lindstrom (8) concluded that locule number did not appreciably influence fruit weight, with equatorial diameter held constant. Since equatorial diameter itself is a measure of size and perhaps also partly the effect of locule number, in this study the shape index is used instead of equatorial diameter. While the data of Table III show significant correlations between locule number and weight, these are not so large

TABLE III

Simple and partial correlations between locules, weight and shape in F_2 populations and backcrosses involving small oblate many-loculed and large oval 2-loculed tomato varieties.

Number of plants	Pedigree		Locules and shape	Locules and shape (Weight eliminated)	Locules and weight	Locules and weight (Shape eliminated)	Weight and shape	Weight and shape (Locules eliminated)
A								
87	(10) Large Lc o / (36) Small lc O'	F_2	.84**	.82**	.47**	.41**	.31**	-.16
B								
44	(9) Large Lc o / (35) Small lc O	F_2	.65**	.55**	.68**	.59**	.41**	-.04
C								
28	(9) Large Lc o / (36) Small lc O	F_2	.85**	.91**	.32	.70**	-.06	-.66**
D								
203	(9) Large Lc o / (36) Small lc O	x (50) Large lc o / Large lc o	.70**	.79**	.49**	.65**	.03	-.50**
E								
70	(10) Large Lc o / (35) Small lc O	x (50) Large lc o / Large lc o	.88**	.92**	.62**	.69**	.36**	-.50**
F								
47	(9) Large Lc o / (36) Small lc O	x (40) Large lc O / Large lc O	.31*	.31*	.17	.18	.00	-.60**

	Numb			Loc	Loc (Wei	Loc	Loc (Sh	Wei	Wei (Loc
A	87	(10) Large Lc o / (36) Small lc O'	F_2	.84**	.82**	.47**	.41**	.31**	-.16
B	44	(9) Large Lc o / (35) Small lc O	F_2	.65**	.55**	.68**	.59**	.41**	-.04
C	28	(9) Large Lc o / (36) Small lc O	F_2	.85**	.91**	.32	.70**	-.06	-.66**
D	203	(9) Large Lc o / (36) Small lc O x (50) Large lc o / Large lc o		.70**	.79**	.49**	.65**	.03	-.50**
E	70	(10) Large Lc o / (35) Small lc O x (50) Large lc o / Large lc o		.88**	.92**	.62**	.69**	.36**	-.50**
F	47	(9) Large Lc o / (36) Small lc O x (40) Large lc O / Large lc O		.31*	.31*	.17	.18	.00	-.60**
G	58	(15) lc o / (51) Lc O x (15) lc o / lc o		.79**	.79**	.69**	.69**	.38**	-.85**

as those between locule number and shape. This phenotypic association of locule number and shape has led to the work on the inheritance of locule number set forth later in this paper.

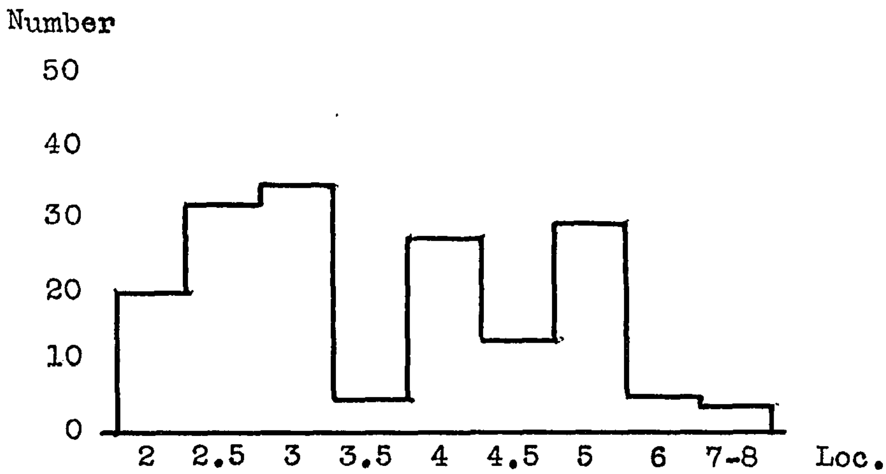
Quantitative characters are more difficult to classify than qualitative ones, as usually the transition from one class to another is not abrupt. Nevertheless, if such characters are largely the result of major single genes, a classification of F_2 and back-crossed plants should show a somewhat definite segregation. Figure 1 depicts graphs of the distribution of F_2 and back cross populations from crosses between few-loculed and many-loculed plants. In both cases there are bi-modal distributions with the low point falling at 3.5 locules. This, together with the fact that in crosses between (2-3)-loculed varieties and many-loculed ones the F_1 is (2-3)-loculed, suggests this as a natural point of division between <u>lc</u> (many-loculed) and <u>Lc</u> (few-loculed). In the case of the F_2, approximately three-fourths (133) of the population would thus be classed as Lc and one-fourth (49) as lc, which fits a Mendelian 3-1 ratio with P = .74. In the back crosses the division of the population above and below this point is in the proportion of 1-1, namely 84-83. A single major gene for locule number is therefore proposed.

Theoretically, if locule number is due to a gene independent of that causing locule shape, the production of a tomato variety carrying the <u>o</u> gene together with <u>lc</u> should be

(A)

Combined

$\frac{15}{\text{Sunrise}}$ x 15 and $\frac{15}{\text{Red Pear}}$ x 15 (Back Crosses)



(B)

$\frac{\text{Bison}}{\text{Yellow Pear}}$ F_2

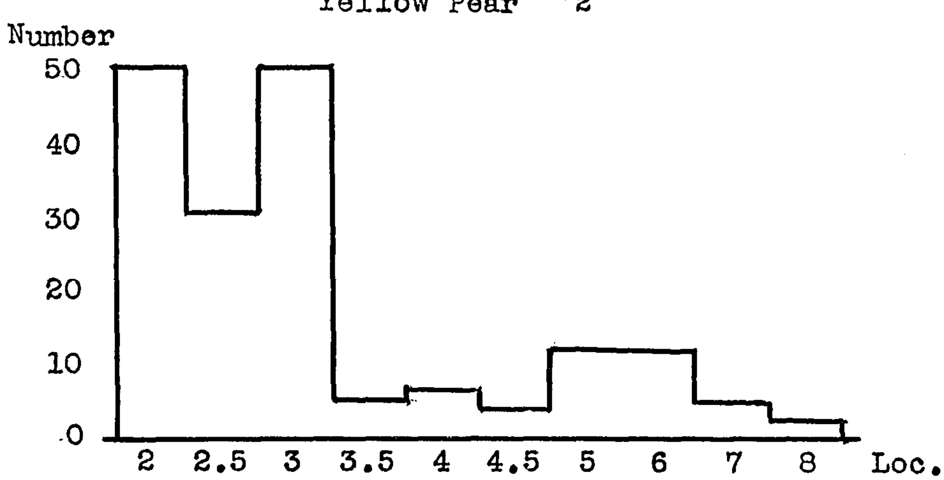


Figure 1
Segregation of progenies according to locule number. Of the parental stocks used, Sunrise, Yellow Pear and Red Pear were (2-3)-loculed, 15 was (4-5)-loculed, and Bison was (4-8)-loculed.

possible. Steps were taken to synthesize such a variety and the outcome was a success. In the meantime a pure variety seeming to have the same combination was selected from a strain from J. W. Lesley of California. This was used because it also carried the recessives d and s. This form, carrying genes for oval and many-locules, had phenotypically round fruit, according to our hypothesis because the added locules offset the phenotypic effect of o. Table IV-A and B gives the F_2 data of this tomato (No. 15) crossed with two varieties (Sunrise and No. 52) carrying Lc and the oblate gene O. The F_2 should, if the hypothesis is correct and linkage not too great, give some plants which would be o Lc, and the fruit therefore oval. These did occur, as may be noted in the table.

A back cross between the F_1 and dd, oo, ss, lclc shown in Table IV-C lends support to the F_2 data. Here we have the appearance of oval, two-loculed tomatoes from parents both of which were phenotypically round.

Assuming that the round, many-loculed tomato in Table IV (No. 15) did carry oo but, because of many locules was phenotypically round, and that many locules are recessive to few, a cross between it and an LcLc oo tomato should give in the F_1 not a round but an oval (2-3)-loculed fruit. Such a cross is shown in Table V where it will be noted the F_1 fulfills expectations. The F_2 and back cross tabulations disclose no 2-loculed, round-fruited plants such as were noted

TABLE IV

F_2 and back cross populations showing the appearance of oval tomatoes from crosses between two phenotypically round tomatoes which differ genetically, both in locule shape and number.

$$\frac{\text{(Sunrise)}\ \underline{O}\ \underline{Lc}}{(15)\ \ \underline{o}\ \underline{lc}}\ F_2$$

(A)

Locules	.60	.65	.70	.75	.80	.85	.90	.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	Ratio $\frac{L}{W}$ Total
2.0				1	4	8	8	1	4	1	4	1	1	2	1		36
2.5				2	8	5	5	3	1								29
3.0		1	2	3	9	18	6	5	6								50
3.5				1		3	1										5
4.0			1	2		3	5	1	1	1							14
4.5				1	1	1	1										4
5.0			5	5	8	5											23
6.0			2	1													3
7.0				1													1
Total		1	10	17	30	43	26	10	12	2	4	1	1	2	1		

$$\frac{(52)\ \ \underline{O}\ \underline{Lc}}{(15)\ \ \underline{o}\ \underline{lc}}\ F_2$$

(B)

Locules	.70	.75	.80	.85	.90	.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	Ratio $\frac{L}{W}$ Total
2			1	4	8	3	9		3	3	1	2	2	36
3		1	4	3	2	1		3	2	1				17
4		1	1	1	3									6
5		1		1	0	1								3
6		1			1									2
7	1													1
Total	1	4	6	9	14	5	9	3	5	4	1	2	2	

$$\frac{(15)\ \ \underline{o}\ \underline{lc}}{\text{(Sunrise)}\ \underline{O}\ \underline{Lc}} \times (15)\ \frac{\underline{o}\ \underline{lc}}{\underline{o}\ \underline{lc}}\ \text{Back cross}$$

(C)

Locules	.70	.75	.80	.85	.90	.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	Ratio $\frac{L}{W}$ Total

4.5			1	1	1	1									4
5.0		5	5	8	5										23
6.0		2	1												3
7.0			1												1
Total	1	10	17	30	43	26	10	12	2	4	1	1	2	1	

$$\frac{(52)\ \underline{O\ Lc}}{(15)\ \underline{o\ lc}}\ F_2$$

(B)

Locules	.70	.75	.80	.85	.90	.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	Ratio $\frac{L}{W}$ Total
2			1	4	8	3	9		3	3	1	2	2	36
3		1	4	3	2	1		3	2	1				17
4		1	1	1	3									6
5		1		1	0	1								3
6		1			1									2
7	1													1
Total	1	4	6	9	14	5	9	3	5	4	1	2	2	

$$\frac{(15)\ \underline{o\ lc}}{(\text{Sunrise})\ \underline{O\ Lc}} \times (15)\ \frac{\underline{o\ lc}}{\underline{o\ lc}}\ \text{Back cross}$$

(C)

Locules	.70	.75	.80	.85	.90	.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	Ratio $\frac{L}{W}$ Total
2.0				2	3	2			1		1	1			10
2.5		1	3	1	2	3	1		3	3		1	1	1	20
3.0			1	5	5	2	7	3	2	1					26
3.5				1			1								2
4.0	1	1	2	3	4	1	2	2	1						17
4.5		1	2		1	3		1							8
5.0			7	4	3	1	2								17
6.0			1		1	1									3
8.0	1														1
Total	2	3	16	16	19	13	13	6	7	4	1	2	1	1	

TABLE V

F_2 and back cross populations showing association between locule number and shape where both parental stocks are genetically oo, but differ in locule number.

$$\frac{\text{(Red Pear)}}{(15)}\ \frac{\underline{o}\ \underline{Lc}}{\underline{o}\ \underline{lc}}\ F_2$$

Locules	.75	80	85	90	95	100	105	110	115	120	125	130	135	140	145	150	155	160	180	$\frac{L}{W}$	Total
2								1	17	6	16	13	9	14	8	8	2	2	1		97
3						1	1	5	2	4	1	0	2								16
4			1	2	1	6	2														12
5	1	0	2	1	2	2															8
6		1	1	2																	4
7	1																				1
Total	2	1	4	5	3	9	3	6	19	10	17	13	11	14	8	8	2	2	1		

$$\frac{(15)}{\text{(Red Pear)}}\ \frac{\underline{o}\ \underline{lc}}{\underline{o}\ \underline{Lc}} \times (15)\ \frac{\underline{o}\ \underline{lc}}{\underline{o}\ \underline{lc}}\ \text{Back cross}$$

Locules	85	90	95	100	105	110	115	120	125	130	135	140	145	150	155	---	180	$\frac{L}{W}$	Total
2.0										1	4	2			2		1		10
2.5								1	2	3	3		1	1					11
3.0					1		2			1	3								7
3.5					1				1										2
4.0				2	3	3		1			1								10
4.5				2						1									3
5.0		1		4	3	1	2												11
6.0	2																		2
8.0	1			1															2
Total	3	1	0	9	8	4	4	2	3	6	11	2	1	1	2		1		

		$\frac{\text{Length}}{\text{Width}}$ Ratio	Locule No.
P_1	15-2 -	.95	4-5
P_1	Red Pear -	1.33	2-3
F_1	15-2x Red Pear -	1.34	2-3

in Table IV, nor any many-loculed ovals, but as the number of locules increases the shape index changes.

Data have already been presented in Table I which suggest linkage between locule number and first chromosome genes. Table VI gives data showing the amount of this linkage with Ss and Dd. These furnish a basis for the location of Lclc on the chromosome map. Each population shows linkage between Lclc and Ss with a mean cross-over percentage of 20.5. Between Lclc and Dd, however, there is a mean cross-over percentage of 46.9. From these data it would seem safe to suggest that there is a gene for increased locule number (lclc) linked with one for compound cluster (ss) and that it's locus is on the opposite end of the chromosome from Dd. With a 20.5 per cent crossover value between Lclc and Ss, as calculated here, and more than 30 units between Dd and Ss according to MacArthur, the linkage between Dd and Lclc should be very slight, as the figures in Table VI show.

TABLE VI.

Linkage relations of lc to s and d, in back cross coupling, F_2 coupling, and F_2 repulsion phases.

Parentage	S Lc	S lc	s Lc	s lc	Crossover Value	X^2 2 x n	P
(52) S Lc / (15) s lc F_2	48	3	5	9	.142±.026	25.7	.01-
(Sunrise) S Lc / (15) s lc x (15) s lc / s lc	42	12	14	36	.250±.034	29.3	.01-
(Sunrise) S Lc / (15) s lc F_2	102	24	15	27	.248±.039	37.89	.01-
(26) S lc / (3) s Lc F_2	152	59	37	4	.325±.05 6	6.02	.02
(Red Pear) S Lc / (15) s lc x (15) s lc / s lc	23	5	4	26	.155±.043	27.5	.01-
(Red Pear) S Lc / (15) s lc F_2	104	5	10	20	.108±.028	61.47	.01-

Parentage	D Lc	D lc	d Lc	d lc	Crossover Value	X^2 2 x n	P
(Sunrise) D Lc / (15) d lc x (15) d lc / d lc	30	24	26	23	.478±.05	.063	.80
(Sunrise) D Lc / (15) d lc F_2	91	43	26	8	.561±.05	1.313	.25
(26) D lc / (3) d Lc F_2	137	60	52	3	.240±.03	9.820	.01-

$\frac{\text{(Red Pear) } \underline{S}\ \underline{Lc}}{\text{(15) } \underline{s}\ \underline{lc}} \times (15)\ \frac{\underline{s}\ \underline{lc}}{\underline{s}\ \underline{lc}}$	23	5	4	26	.155±.043	27.5	.01-
$\frac{\text{(Red Pear) } \underline{S}\ \underline{Lc}}{\text{(15) } \underline{s}\ \underline{lc}}\ F_2$	104	5	10	20	.108±.028	61.47	.01-

Parentage	D Lc	D lc	d Lc	d lc	Crossover Value	X^2 2 x n	P
$\frac{\text{(Sunrise) } \underline{D}\ \underline{Lc}}{\text{(15) } \underline{d}\ \underline{lc}} \times (15)\ \frac{\underline{d}\ \underline{lc}}{\underline{d}\ \underline{lc}}$	30	24	26	23	.478±.05	.063	.80
$\frac{\text{(Sunrise) } \underline{D}\ \underline{Lc}}{\text{(15) } \underline{d}\ \underline{lc}}\ F_2$	91	43	26	8	.561±.05	1.313	.25
$\frac{\text{(26) } \underline{D}\ \underline{lc}}{\text{(3) } \underline{d}\ \underline{Lc}}\ F_2$	137	60	52	3	.240±.03	9.820	.01-
$\frac{\text{(Red Pear) } \underline{D}\ \underline{Lc}}{\text{(15) } \underline{d}\ \underline{lc}} \times (15)\ \frac{\underline{d}\ \underline{lc}}{\underline{d}\ \underline{lc}}$	14	22	14	8	.620±.06	3.566	.06
$\frac{\text{(Red Pear) } \underline{D}\ \underline{Lc}}{\text{(15) } \underline{d}\ \underline{lc}}\ F_2$	82	16	32	9	.448±.06	.322	.60

The Development of Shape

In connection with the study of the inheritance of shape and size in tomatoes, measurements were made of the length and width of the ovaries at the time of anthesis, and these measurements were compared with similar measurements of mature fruits from the same plants. The correlations between such measurements are shown in Table VII for an F_2 population of a cross between Yellow Pear, small oval; and Bison, large oblate, and similar figures for a group of plants of many varieties, excluding Ohio Red and Oxheart for reasons given later. The correlation between the shape of ovary and the shape of the mature fruit is very striking. It is so great that it would seem probable that such measurements might be a better indication of the actual genetical constitution of the plant than the measurement of mature fruits, since the amount of seed and later growing conditions have considerable effect upon the shape of the fruit when mature.

TABLE VII

Correlations between ovary measurements at anthesis and mature fruit measurements.

POpulation	Number of plants	Ovary and fruit correlations		
		Length	Width	Ratio $\frac{L}{W}$
$\frac{\text{(Yellow Pear) o}}{\text{(Bison)}}$ F_2	179	.594**	.853**	.923**
Miscellaneous Varieties	78	.619**	.639**	.903**

These data are in accord with those of Hackbarth et al. (3) who found a high degree of correlation between size of tomato ovaries and mature fruits. Houghtaling (5) explains this as the result of a differential growth rate which exists from earliest primordia until anthesis by which time cell division is completed. Increase in size thereafter is due to an increase in cell size. Contrasted to this is the condition in Cucurbita as reported by Sinnott and Kaiser (15), where differences in fruit shape are existant at earliest primordia and in Capsicum where differences appear after anthesis. A condition similar to that in Cucurbita is also reported in cucumbers by Hutchins (6) and in watermelons by Weetman (19).

Pear shape has been something of a puzzle since the earliest genetical work with tomato. It was first used as the designation for lengthened fruit shape but was later replaced by the oval gene. While an examination of developing ovaries reveals that oval shape may be detected long before anthesis, pear is often not evident until near blooming time. At anthesis in pear varieties, the ovaries have the appearance of being molded into pear form by the constricting effect of the cone forming corolla tube around the pistil. Longitudinal sections at various times show that the seed cavities extend internally into the base of the ovary until the external, necked appearance is visible under a hand lens (see Fig. 2). Genetically identical stocks raised in different environments may vary in the degree of pear shape in mature fruits. For example, two groups of plants of a red pear variety were raised, one in the field and the other in the greenhouse. The crop in the field was typically pear shaped, the one inside had few distinctly pear shaped fruits. Even on the same plant some specimens may be markedly pear shaped and others oval but not pear. Occasionally fruits may be grooved in the middle or with the neck of the fruit showing an added constriction. When these were first seen on plants in practical breeding blocks the plants were discarded as being rogues, but, an examination disclosed remnants of the corolla tube. This suggested that pear shape might be induced by the fused corolla tube. If this is so, an early removal of the corolla should result in fruits without a neck. Such an operation on blossoms of the pear tomato did produce this effect in some cases as will be noted in Figure 2-H. Pear shape may therefore be a secondary effect of a constricting corolla. This does not mean that this tendency is not inherited, but it does throw some light on the reason why its inheritance is difficult to study. Not only was pear shape not evident in some fruits developing from flowers the corolla tube of which was removed early, but in several instances, such as the one shown in Figure 2-H, the resulting fruit was round rather than oval, suggesting that oval itself may be an induced condition.

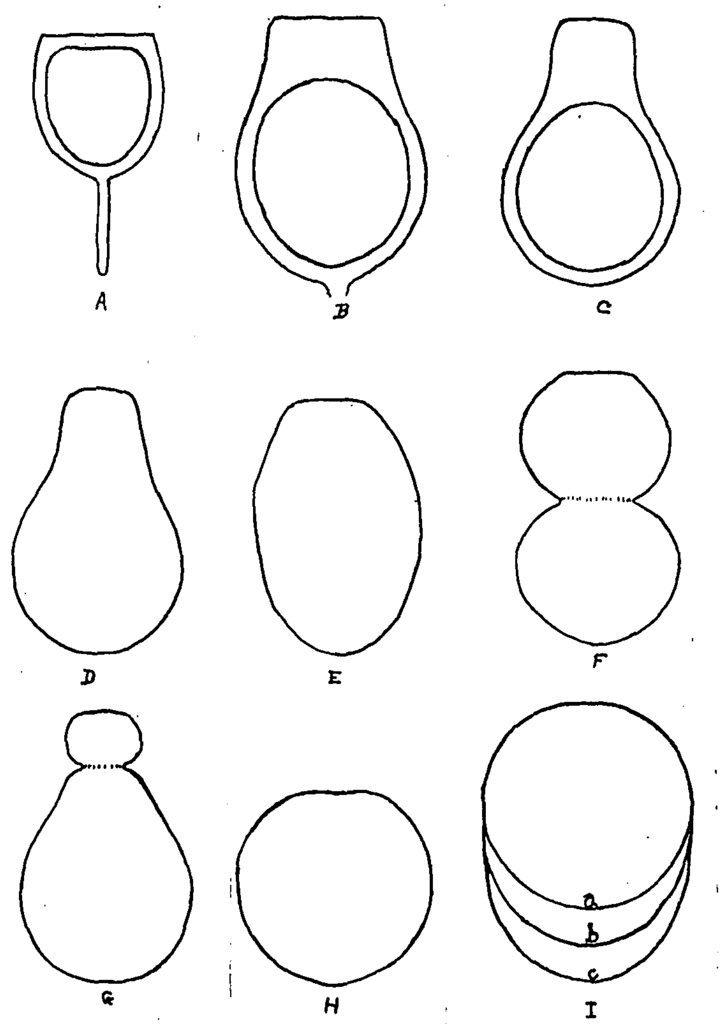


Figure 2
A, B and C - Diagrams showing the development of pear shape; A a considerable time before anthesis, B at anthesis, C mature fruit. The shift in locule location may be noted.
D, E, F and G - Fruit shape variations to be found on the same plant. F and G are undoubtedly due to persisting corolla tube constriction.
H - Fruit resulting from a blossom of pear variety from which the corolla tube was removed some time before anthesis.
I - Shape changes in large oval tomatoes such as Ohio Red; a-at anthesis, b-blossom faded, c-from 1/3 mature fruit length to maturity.

Another Oval Fruit Shape

In the inheritance of size and shape the Ohio Red variety was used because it is large in size, nearly oval in shape, and carries several locules per fruit. One of the first crosses made with this variety was between it and a tomato which was dd rr oo LcLc. In the F_2 from such a cross, as shown in Table VIII-A, there were 64 plants among 256 which were classed as oblate, and an additional 75 which were round. The appearance of oblate-fruited plants in the F_2 in crosses between these two oval varieties would indicate that the two ovals are not due to the same gene. Inasmuch as there was some possibility that the Ohio Red used in this cross was not genetically pure another cross was made between Yellow Plum and a new stock of Ohio Red obtained from the Department of Genetics of Iowa State College which had been carried through several generations and found pure. The tabulation of the F_2 from this seed is shown in Table VIII-B. Here again six of the 47 plants carried decidedly oblate fruits and five more round.

TABLE VIII

Segregation of oblate tomatoes from crosses between small oval and large oval varieties.

Pedigree	Total Plants	$\frac{L}{W}$ Oblate -.99-	Round 1.0-1.2	Oval 1.2 and Above
(A) $\frac{\text{(Ohio Red) large, oval}}{\text{(3) small, o}}$ F_2	256	64	75	117
(B) $\frac{\text{(Ohio Red) large, oval}}{\text{(Yellow Plum) small, o}}$ F_2	47	6	5	36

Further evidence for the belief that the large oval differs from o is found in the fact that while crosses between oo tomatoes and OO two-loculed varieties produce an oblate F_1, Ohio Red in such cases gives an intermediate slightly oval ($\frac{L}{W}$ = 1.1).

Correlations between ovaries and fruits in an F_2 cross between Ohio Red and an OO lclc variety are listed in Table IX. It will be noted that ovary width and fruit width are here correlated much the same as before but that ovary length and fruit length are not significantly correlated. The shape correlation is similar to that for width and far less than that found for other varieties in Table VII.

TABLE IX
Correlation of ovary and fruit measurements in a cross involving large oval.

$\frac{(53)}{\text{(Ohio Red)}}\ \frac{o}{\text{large oval}}\ F_2$ N=61

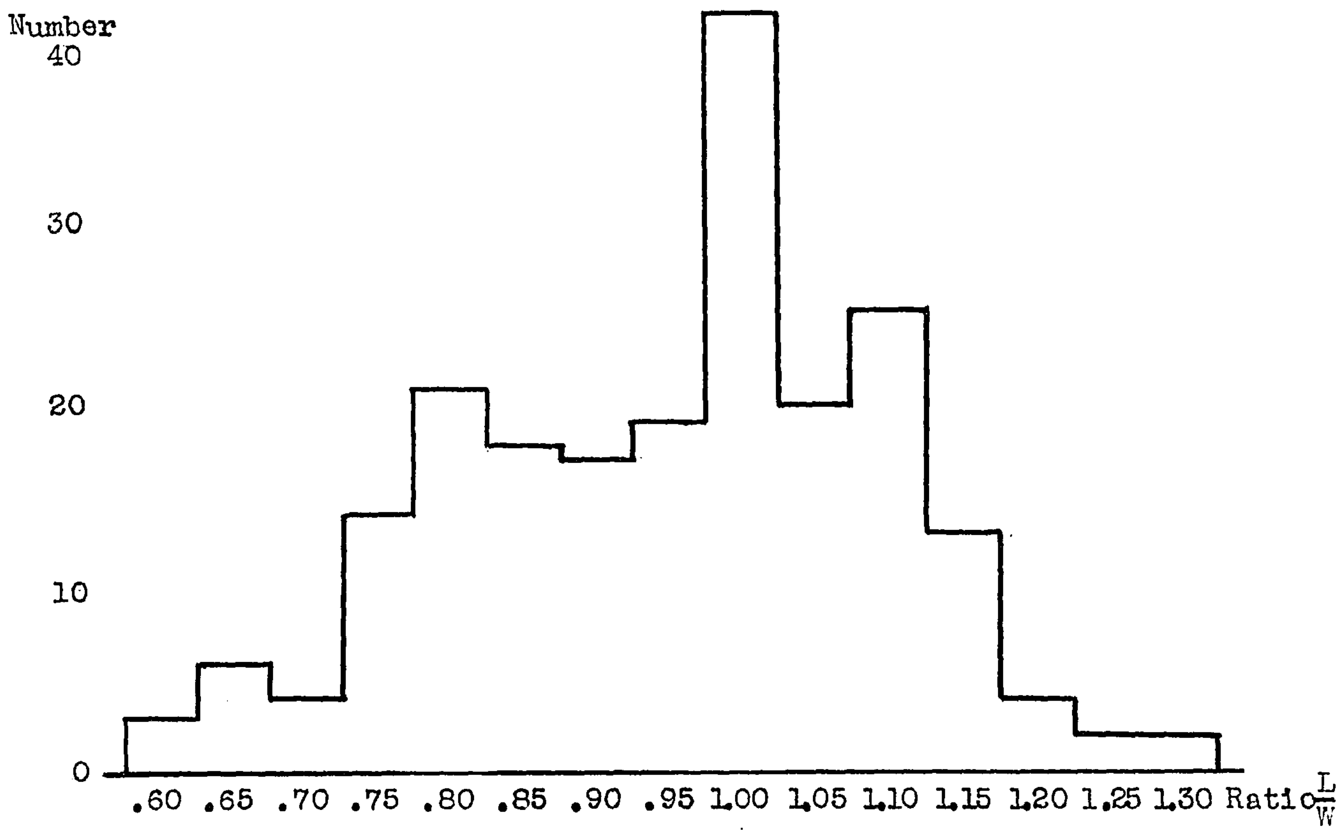
Correlation length, ovary and fruit	.038
Correlation width, ovary and fruit	.694**
Correlation ratio, $\frac{L}{W}$, ovary and fruit	.598**

The reason for this lack of length correlation was disclosed by a study of the developing ovaries in the F_1 individuals of a cross between Ohio Red and the variety OO LcLc in which it was found that at anthesis the ovary was round, but that the polar diameter increased relatively faster than the equatorial until the tomatoes are about one-third of their full length, the result being an elongated fruit (See Fig. 2-I).

These studies with this large oval variety thus indicate that its shape is not due to o, but to a partially dominant gene or genes whose differentiating effect is produced after anthesis. The inference is that the differential growth rate which Houghtaling (5) found to cease at anthesis continues much longer in this case. Histological studies show that the number of cells is greatly increased after this time. For convenience and in order to differentiate this gene or genes from O and o the symbols Ee are proposed in which E indicates the presence of continued elongation and e its absence.

If E is distinct from o, the question arises as to whether it is due to a single gene. A cross between Ohio Red, EE, and Red Currant, ee, produced, in the F_2, 157 plants with fruits visibly longer than broad, and 48 round or oblate. This approaches a 3-1 ratio. Two other F_2 populations from crosses between Ohio Red and oblate, many-loculed, varieties were classified by appearance only. These gave 74 E, 52 e; and 92E, 68 e respectively. These are, obviously, not 3-1 ratios. Hence, it appeared either that E was not due to a single gene or else its classification in this way was unsatisfactory. A cross was therefore made between Ohio Red and Yellow Cherry for the purpose of a more careful analysis. The F_2 is plotted graphically in Fig. 5-A. Its distribution suggests multiple factors and can hardly be explained on the basis of a single gene. The mean $\frac{L}{W}$ ratio of .96 in the F_2 as compared to 1.08 in F_1 also indicates a complex situation or the influence of dominance. A back cross involving E and a large oblate variety is shown in Fig. 5-B. The bimodal curve there is suggestive of a single factor. The mean of the back cross is $\frac{L}{W}$ = .91, which is much below that of the F_1. It is possible this segregation into two classes may be due to differences in locule number rather than to continued elongation since the large oblate used carries many more locules than Ohio Red.

(A)



(B)

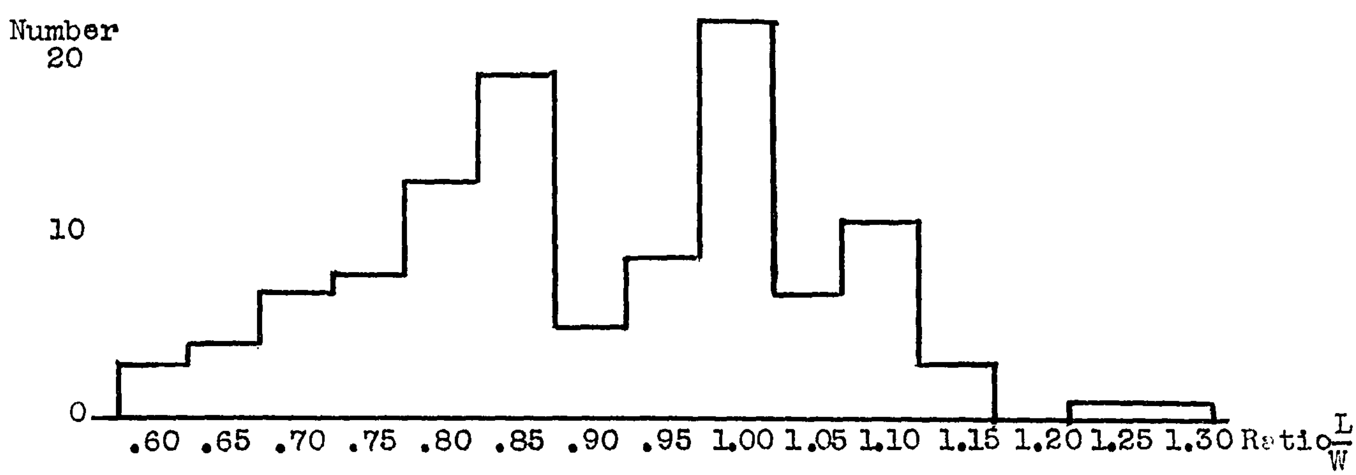


Figure 3

A - The shape distribution of the F_2 population from a cross between Ohio Red and Yellow Cherry.

B - The shape distribution of a population from Ohio Red x (40), an oblate many loculed variety, back crossed to (40).

Even though we accept this elongation as the probable result of multiple factors, we might still, through shape association with other genes, learn something of its component parts. Table X gives a compilation of crosses made for this purpose.

TABLE X
Shape association in crosses involving large oval (E) and the genes Dd Aa Ll Cc Rr Spsp and Yy.

Pedigrees	Number	Gene	Ratio $\frac{L}{W}$	Difference	P
(Ohio Red) DALCRYE / dalcrye (29) x (29) dalcrye / dalcrye	130 126	D d	.80±.011 .76±.014	.04±.02	.04
	115 140	A a	.79±.021 .78±.011	.01±.02	.62
	133 123	L l	.79±.011 .77±.012	.02±.02	.32
	142 114	C c	.79±.011 .76±.012	.03±.02	.13
	102 154	R r	.76±.021 .79±.011	.03±.02	.13
	126 130	Y y	.77±.021 .79±.012	.02±.02	.32
Back Cross (Ohio Red) DRSpE / drspe (40) x (40) drspe / drspe	52 61	D d	.93±.020 .88±.018	.05±.027	.07
	53 60	R r	.89±.020 .92±.019	.03±.027	.49
	55 58	Sp sp	.91±.020 .90±.019	.01±.027	.58
F_2 (Ohio Red) R Lc E / (Yellow Cherry) r lc e	155 52	R r	.935±.013 .938±.013	.003±.026	.90

There is, in Table X, no satisfactory evidence that elongation (E) is associated with any of the genes for which it is tested there. Even the apparent possible association with Dd may be due to the association of Dd with differences in locule number which are present in the parent stocks.

DISCUSSION

Any study of the inheritance of fruit size and shape in the tomato plant reveals that the matter is complex. Environment is known to affect both characters in other species of fruits. For example, apples of the same variety are much lengthened in the western United States as compared to the upper Mississippi Valley. The vegetative vigor of a plant greatly affects the size of fruit. This being true, genes not directly related to size and shape of the fruit in such a plant as the tomato but which affect its general vigor and other plant characteristics, as suggested by MacArthur (12), have their effect. When genetically different plants are grown under different environments where there is variation in external conditions, such as temperature, light, soil, and parasites, the effect of the different genes will be modified. Even on the same plant, conditions differ enough in different parts to affect size and shape.

During the six years of this investigation many tomato crosses weremade and studied in an attempt to learn more about the development and inheritance of fruit shape and size. It was found that there is a high degree of association between locule number, size and shape, and that an association exists between qualitative first chromosome factors and locule number.

By means of partial correlations the existing correlations between shape and weight were shown to be due at least in part to their mutual correlation with locule number. Locule number was found to segregate in a ratio of 3:1 of few to many-loculed plants in F_2 populations, and in a ratio of 1:1 in back crosses, the dominant group carrying 2-3 locules and the recessive group $3\frac{1}{2}$ and more locules.

A round tomato with many locules has been shown to be oo lclc by means of crosses of it with two-loculed round tomatoes and two-loculed oval tomatoes. Linkages with first chromosome genes were calculated which demonstrate that the Lclc locus is on the opposite end of the chromosome from Dd beyond the locus of Ss. The presence of this gene for locule number may have an effect on size by an increase or decrease in the number of locules without affecting their size. This relationship is not fully demonstrated and even if it were it would not account for all size differences. Obviously there are other size genes, since oval two-loculed tomato fruits are known which are several times larger than others. The same is true of round two-loculed sorts. More work is needed on the locule number and size relationship.

The existence of the gene Lclc is of great importance in accounting for variations in tomato shape. The shape genes Oo which affect gross fruit shape through their effect on locule shape together with Lclc which affect shape by varying the locule number, provide a key for explaining gradations as follows: OLc = round, Olc = oblate, o Lc = oval, and olc = round.

Correlations between measurements of ovaries and mature fruits have confirmed the findings of others that with most varieties the size and shape of tomatoes is predictable at blossoming time by measuring the ovaries. Observations have shown marked effects of environment on pear shape. Mature fruits have been observed in which a persistent corolla tube has obviously caused constrictions. Early removal of the corolla has resulted in fruits without pear shape on plants where control blossoms produced pear fruits. These suggest that pear shape is probably induced by the constricting effect of the fused corolla tube.

The importance of such developmental studies is emphasized by the differentiation of two groups of oval tomatoes recorded in this paper. The one type symbolized by o is composed of the usual comparatively small-fruited varieties in which the final shape and size is fixed at blossoming. The other, including the larger-fruited varieties, is due to a probable complex which causes continued elongation symbolized by Ee. When this is superimposed on a round tomato, it becomes oval, on an oval tomato extreme length results, but when added to an otherwise oblate tomato the result is round. The nature of this complex and its inheritance has not been cleared up. In order to clarify this it would seem desirable to use only LcLc varieties for both parents. This would require either the discovery of, or the synthesis of a pure elongated LcLc stock which might require considerable time and labor. If this were to be done it is possible that the existence of a single gene for continued elongation could be demonstrated. Such confusion as has been observed to date may be only the effect of Oo, Lclc, and perhaps other recognized genes such as Ff.

Practical breeding work has demonstrated the possibility of recombining Oo, Lclc, and Ee. Comparatively large, very oval, few-loculed varieties from Iowa State College, apparently oo LcLc EE, when crossed with Early Jumbo, OO lclc ee, have resulted in varieties closely resembling Oxheart, which we believe to be OO lclc EE. Oxheart, a large OO lclc EE plant, crossed with Yellow Cherry, a small OO LcLc ee plant, resulted in segregates which were very oblate, small many-loculed, with the probable formula OO lclc ee. Ohio Red, OO lclc EE, crossed with Yellow Pear, oo LcLc ee, has given very long comparatively large segregates, oo LcLc EE. While these examples are not offered as a definite proof of a single gene for added elongation they do point toward a reasonably simple complex.

CONCLUSIONS

1. There is significant correlation between shape, size and locule number in tomato fruits. The correlation between shape and size is partly due to their mutual correlation with locule number.

2. A major gene for locule number exists. *Lc*, 2-3 locules, is dominant over *lc*, $3\frac{1}{2}$+ locules.

3. The locus of *Lclc* is on the first chromosome about 20 crossover units beyond *Ss*.

4. The effect of *lc* when associated with *o* is to produce a phenotypically round tomato.

5. With most of the tomato varieties, the size and shape of the matured fruit are predictable from ovary measurement at anthesis.

6. Pear shape is probably due to the constricting effect of the fused corolla tube.

7. Oval tomatoes in some cases are the result of genes other than *o*, whose effect is to continue the elongation of the ovary after anthesis.

LITERATURE CITED

1. Currence, T. M. Genetic association between qualitative and quantitative characters in the tomato. Proc. Sixth Intl. Cong. of Gen. 2:32-34. 1932.

2. Frimmel, Franz. Über die Vererbung der Fruchtgrosse der Tomaten, Zeitsch. Pflanzenzüchtung 8:457-462. 1922.

3. Hackbarth, J. Loschakowa-Hasenbusch and V. Sengbusch R. Die Züchtung fruhriefer Tomaten mittels Kreuzungen zwischen Solanum lycopersicum and Solanum racemigerum. Der Züchter 5:97-105. 1934.

4. Hedrick, U. P. and Booth, N. O. Mendelian characters in tomatoes. Amer. Assoc. Hort. Sci. rept. 1907:19-24. 1908.

5. Houghtaling, Helen B. A developmental analysis of size and shape in tomato fruits. Bul. Torrey Bot. Club 62:243-252. 1935.

6. Hutchins, A. E. Morphological relationships in the ontogeny of the cultivated cucumber, Cucumis sativus L., Minn. Agr. Exp. Sta. Tech. Bull. 96. 1934.

7. Leslie J. W. and Rosa, J. T. The improvement of tomatoes by selection. Hilgardia 2:25-45. 1926.

8. Lindstrom, E. W. Hereditary correlations of size and color characters in tomatoes. Iowa Agr. Exp. Sta. Res. Bull. 93. 1926.

9. Lindstrom, E. W. The inheritance of ovate and related shapes of tomato fruits. Jour. Agr. Res. 34:961-985. 1927.

10. Lindstrom, E. W. Linkage of size, shape and color genes in Lycopersicum. Zeitschrift Indukt. Abstam. u. Vererb. Supp. 2:1031-1057. 1928.

11. Lindstrom, E. W. Linked inheritance in tomatoes. Iowa State Col. Jour. of Sci. 1:3-14. 1926.

12. MacArthur, J. W. Fruit size effects of qualitative genes in the tomato. Am. Nat. 68:73-74. 1934.

13. MacArthur, J. W. Linkage groups in the tomato. Jour. Gen. 29:123-133. 1934.

14. Price, H. L. and Drinkard, A. W. Jr. Inheritance in tomato hybrids. Va. Agr. Exp. Sta. Bull. 177. 1908.

15. Sinnott, E. W. and Kaiser, Samuel. Two types of genetic control over the development of shape. Bull. Torrey Bot. Club 61:1-7. 1934.

16. Sinnott, E. W. Shape changes during development in Cucurbita and their importance in the study of shape inheritance. Am. Nat. 66:301-309. 1932.

17. Wallace, H. A. and Snedecor, G. W. Correlation and machine calculation. Official Pub. Iowa State College 30:No. 4, Rev. 1931.

18. Warren, P. A. Genetic studies in Lycopersicum. Mich. Acad. Sci. Arts and Letters 4:357-394. 1924.

19. Weetman, Leslie M. Inheritance and correlation of shape, size and color in watermelon. (Abstract) Am. Nat. 52:70. 1936.

ACKNOWLEDGMENT

In the pursuance of this investigation and the preparation of this manuscript, the invaluable advice and assistance of Dr. E. W. Lindstrom have been freely given and are gratefully acknowledged.

VITA

Parents	Chas. D. Yeager
	Mary T. Schimpff
Born	Feb. 12, 1892, Bazaar, Kansas.
Elementary School	Rural No. 28, Bazaar, Chase County, Kansas.
High School	Chase County High School.
Degrees Earned	B.S. Kansas State College, 1912, Horticulture. Albert Dickens in charge of major.
	M. S. Oregon Agricultural College, 1916, Pomology. C. I. Lewis, V. R. Gardner, E. J. Kraus - Leading teachers.